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The Costs of Human Locomotion: Maternal Investment in Child Transport

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ABSTRACT This article investigates maternal investment in child carrying and presents a method for determining when it is energetically advantageous for a mother to carry her child rather than force her child to walk independently. I calculate maternal and child energy consumption while walking and develop correction factors to facilitate making these energy calculations for young children. In addition, I investigate the effect of maternal burdens in addition to the child and of external nutritional support on energy consumption. Since maternal energy is a finite resource, the "decision" to carry a child or force it to walk independently is especially important. This decision can be predicted from the body mass of the mother and child and the child's age. If the mother provides all of the child's nutrition, then the mother should choose to carry her child only when the energy usage of the mother carrying the child is less than the sum of the energy used when the mother and child walk independently. The critical velocity, when the two expenditures are equal, can then be determined. Several general hypotheses are also addressed.

The critical velocity of a 60 kg mother with a 4-year-old child approximately equals the average walking speed of adult humans. For a lighter mother, the critical velocity is reached when her child is 3 years old, while for heavier mother this point is not reached until her child is 6 years old. The effect of burdens in addition to the child's mass is minimal. Nutritional support of the child by agencies other than the mother decreases the age at which the mother should force the child to walk independently. In some cases, especially for the lightest mothers, it is never in the mother's best energetic interest to carry her child. Am J Phys Anthropol 107:71–85, 1998.

Energy has long been recognized as a particularly valuable resource to all creatures (Fisher, 1958) and for none is energy more valuable than the primate mother with her energetically demanding, dependent youngster (Leonard and Robertson, 1992). Adult primate females are particularly energetically constrained because they must provide for offspring which are highly energetically demanding for long periods of development (Kaplan, 1996). While both gestation and lactation demand significant energy expenditures, other forms of maternal care can also tax the energy reserves of the adult female. One particularly expensive form of maternal care is the energetic cost of carrying offspring. Gestational and lactational energy demands have been extensively studied and yet, paradoxically, little attention has been given to the locomotor

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energy requirements of the mother–child dyad even though carrying is the second most costly form of postpartum maternal investment (Altmann and Samuels, 1992). Energy consumption is of critical importance to the ultimate goals of the mother because the health of the current offspring is affected by maternal energy reserves (Kaplan, 1996) and interbirth intervals can be increased by maternal energy depletion (Tracer, 1991), thus decreasing the fitness of the mother. Energy stores are both finite and nonreusable (Borgerhoff Mulder, 1992) and in most ecological situations there are more demands made on energy stores than supply to fulfill them. Decisions regarding allocation are, therefore, required (Borgerhoff Mulder, 1992). To determine these "decision rules," an explanatory framework that posits optimal allocation of resources is needed. Evolutionary ecology, one such framework, allows for hypotheses about particular situations to be addressed within the larger context of Darwinian natural selection theory (Smith, 1983; Smith and Winterhalder, 1992). Optimal or efficient use of energy, whether in the form of management of personal fat reserves (Adair and Popkin, 1992), selection of prey choice (Kaplan and Hill, 1992), or any other process that involves energy utilization is a central tenet of evolutionary ecology (Smith, 1983). Because parental investment in a current offspring has opportunity costs, a conflict of interest develops between parent and child (Trivers 1974).

In an interesting and innovative paper, Altmann and Samuels (1992) explored the difference in energetic cost to the mother of carrying an infant versus forcing it to walk under its own power. In their study, Altmann and Samuels observed the locomotion patterns of feral savanna baboons, *Papio cynocephalus*, and recorded distance traveled, speed traveled, and at what age and velocity infants were carried by their mothers. They discovered that very young infants (<2 months old) were carried all the time, that older youngsters (>2 months, <8 months) were carried when the mother moved at high velocity, and that the oldest infants (>8 months) were seldom carried. Altmann and Samuels proceeded to explain the motivation for these patterns as the minimization by the mother of total energy expenditure of the mother–infant pair. Since a central assumption of their research was that the mother provides all of the nutritional energy required by the offspring, any energy saved by the infant was energy saved by the mother, which she could then devote to other needs.

Although baboons are terrestrial quadrupeds and show a different relationship of energy usage to velocity than bipeds, similar patterns of the minimization of energy expenditure should also be found in humans.

In this article, I explore locomotor energy expenditure (LEE) in humans and determine LEE for various idealized situations. The differences in energy usage between a mother carrying her child and the mother and child walking independently are examined, as are various combinations of mother and child masses and velocity of travel. In all cases, the mothers are not malnourished and they represent no particular ethnic identity or geographic region. These initial simulations are predicated on the simplifying assumption that the mother provides all of the nutrition for the child and that the mother's "goal" is energy conservation. Obviously, either of these two assumptions may be violated to varying degrees in a real example. This simple approach, however, does allow me to generate several hypotheses about carrying patterns in humans.

As an extension of the initial assumptions, I investigate the effect of burdens in addition to the child and of external nutritional support for the child. The addition of burdens in excess of the child's mass increases the amount of energy that the mother requires to locomote and can potentially affect the critical velocity. External nutritional support for the child decreases the child's effective energy use because support provides energy to the child that is not available for use by the mother.

BACKGROUND

Metabolic energy usage

Beginning in the 1950s and 1960s and continuing until today, various researchers have investigated the rate of energy usage by mammals when moving. Taylor et al.

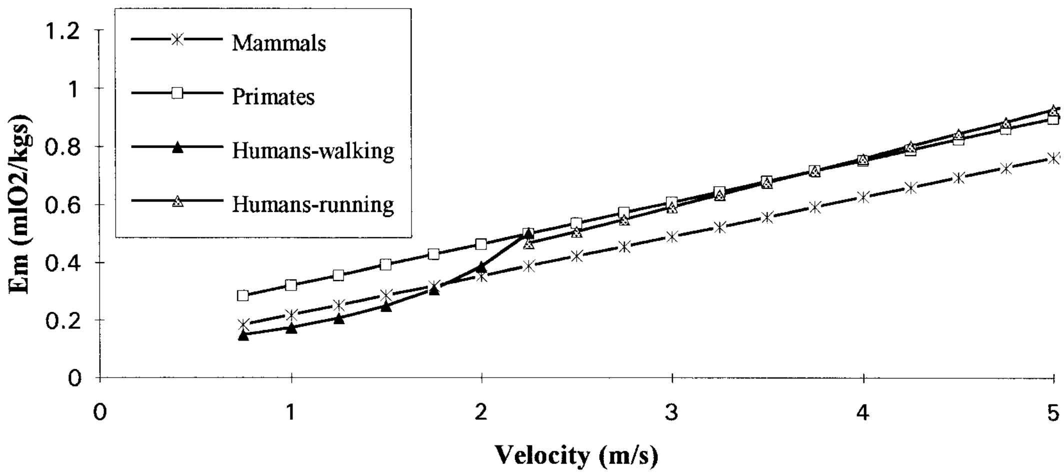

Fig. 1. Energy usage when locomoting versus velocity. Mammals: $Em = 0.3\ m^{-.303} + 0.533m^{-.316}V$. Primates: $Em = 0.345m^{-.157} + 0.523m^{-.298}V$. Humans: $Em = 0.0746\ (1 + V^2)$ (walking); $Em = 0.0168V + 0.0886$ (running). m = mass (kg); V = velocity (m/s).

(1970) demonstrated an interspecific relationship between the body mass of an animal and the energy per kilogram of body mass per meter it used when running. The data used to develop this relationship were gathered using a treadmill to determine velocity and an oxygen analyzer to measure the rate of oxygen consumption. (Oxygen consumption is a measure of the chemical energy used by the body.) The relationship between body mass and energy usage was shown to be a straight line when plotted on a log–log graph. Animals with larger body mass are more efficient on a per kilogram basis than animals with a smaller body mass. This mammalian curve was quickly expanded to include more species and to account for variation in velocity. Taylor et al. (1982) related the metabolic energy usage rate (Em, measured in units of mlO_2/kgs) to the velocity of an animal when locomoting and presented specific curves for various orders, including primates. Other investigators (Cavagna and Kaneko, 1977; Fedak et al., 1982; Heglund et al., 1982a,b) have confirmed and expanded these results. The "average mammal" uses more energy as it increases its velocity, as does the "average primate." Figure 1 shows Em curves for mammals, primates, and humans.

The walking portion of the human curve shown in Figure 1 was developed by Pandolf et al. (1977). It has a distinctly different shape than that of the average mammal or average primate. While the mammal and primate relationships form straight lines in the walking phase, the human relationship is curvilinear. In addition, humans are more efficient at low (walking) velocities than the average mammal or primate. Various investigators have determined Em at different velocities and devised best-fit curves to describe the shape of the Em curve of human walking (Bouchard et al., 1990; FAO/WHO/UNU, 1985; Ferretti et al., 1991; Givoni and Goldman, 1971; Goldman and Iampietro, 1962; Maloiy et al., 1986; Margaria et al., 1963; Minetti et al., 1993, 1994; Pandolf et al., 1977; Pimental and Pandolf, 1979; van der Walt and Wyndham, 1973; Waters et al., 1983, 1988; Workman and Armstrong, 1963; Zarrugh and Radcliffe, 1978; Zarrugh et al., 1974). All of the investigations are essentially in agreement with each other, so only Pandolf et al. (1977) will be detailed herein. A summary of the available data for walking reported in the literature for adult humans is shown in Figure 2. Em drawn from the literature is indicated with open circles while the Pandolf et al. (1977) curve is shown with an unmarked line.

Children use more energy to move a kilogram of body mass than adults do (Silver-

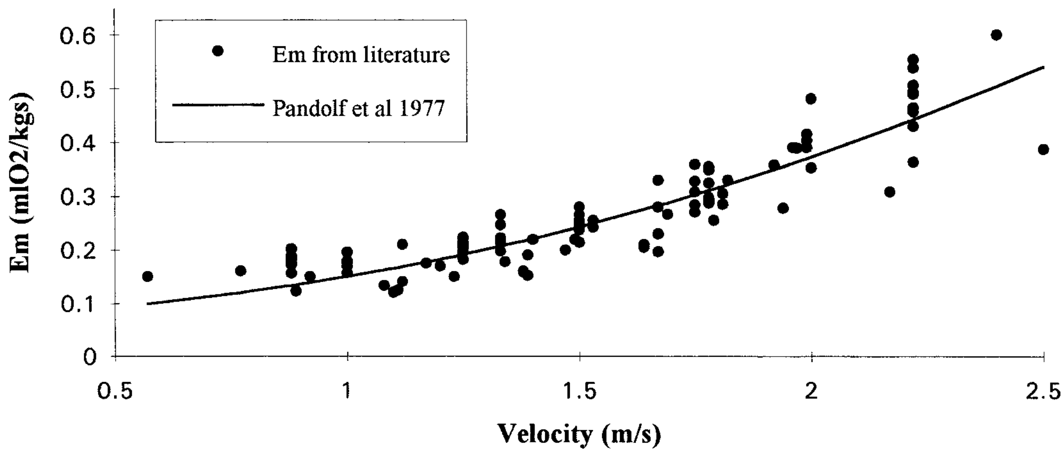

Fig. 2. Empirical data from the literature. Energy used to walk versus velocity. Pandolf et al. (1977): $Em = 0.0746\,(1 + V^2)$.

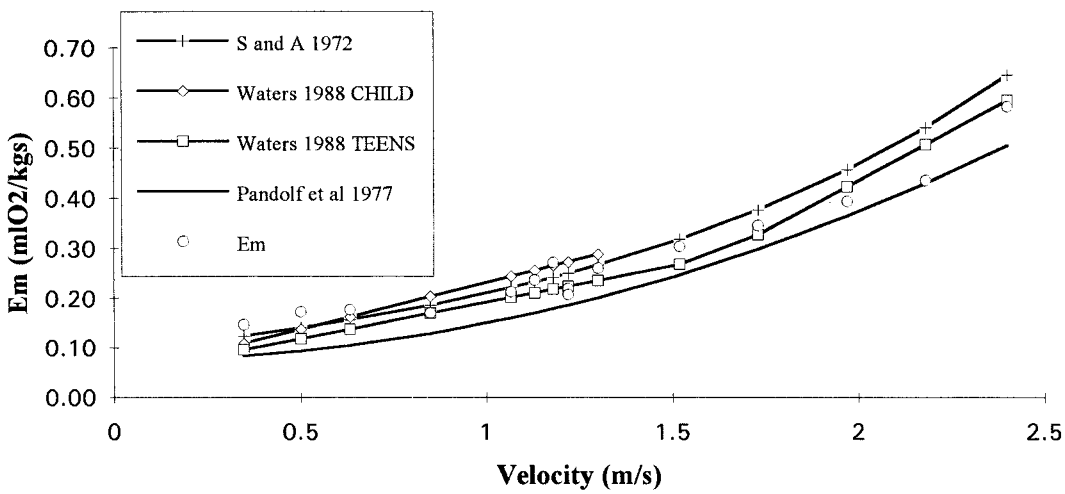

Fig. 3. Empirical data for children from the literature. Energy used to walk versus velocity. Silverman and Anderson (1972): $Em = (10^{.0269V+.751})/60$. Waters et al. (1988) CHILD: $Em = 0.0000522V + 0.0435$. Waters et al. (1988) TEENS: $Em = 0.000408V + 0.0477$ $V < 1.67$ m/s; $Em = 0.000111V - 0.361$ $V > 1.67$ m/s.

man and Anderson, 1972) and the age of the child has a tremendous impact on how much more energy they use than adults. Inefficiency of muscle contraction or limb movements or different body proportions may contribute to this greater usage of energy (Cavagna et al., 1983). Several researchers have evaluated Em of children aged 6–19 years (Rose et al., 1990; Silverman and Anderson, 1972; Waters et al., 1983, 1988). A summary of this research is presented in Figure 3. As before, open circles are data points from the literature; the Pandolf et al. (1977) adult curve, which is shown for reference, is indicated with an unmarked line. Empirical curves developed by Silverman and Anderson (1972) and Waters et al. (1988) are also shown. Silverman and Anderson's (1972) exponential curve was developed from children 6–11 years old and is similar in shape to the Pandolf adult curve. The curves from Waters et al. (1988) are best-fit lines for

children 6–11 years old and teens 13–19 years old. Unfortunately, no empirical data exist for very young children. The only data that are available for young children is an evaluation of their external work (W_{ext}) with respect to the W_{ext} of an adult (Cavagna et al., 1983). External work is the energy required to lift the body center of gravity vertically and to accelerate and decelerate the body. While important, this energy is not the only energy required to walk. Instead, the energy used in walking can be divided into several quantities:

$$\begin{aligned} Em = {} & (\text{Basal Metabolic Rate}) \\ & + (\text{Energy to Stand}) \\ & + (W_{int} + W_{ext}) \\ & + (\text{Energy to Maintain Balance} \\ & \quad \text{and Stability While Moving}). \end{aligned} \tag{1}$$

An approximation of the energy that young children use while walking can be obtained from Cavagna et al. (1983). In their study, children aged 1–10 years were divided into 2-year age groups and the ratio of the children's W_{ext} to the adults' W_{ext} was plotted against velocity.

Factors other than body mass and age of the individual can potentially affect Em. Because one component of Em is basal metabolic rate (BMR), anything that affects BMR also affects Em. BMR represents the minimum amount of energy needed to sustain life and is typically measured on an individual who is sleeping quietly. A correlate of BMR is resting metabolic rate (RMR), which is measured on an individual who is lying quietly. BMR and RMR can vary with many factors. Age and sex of the individual affect both BMR and RMR (FAO/WHO/UNU, 1985). Body composition (percentage of body mass that is fat) affects RMR, perhaps because fat is inert tissue, i.e., does not consume as much oxygen as metabolically active tissue; therefore, a person who has a higher percentage of fat has a lower RMR than a leaner person of the same body mass (Albu et al., 1997; Geliebter et al., 1997; Macor et al., 1997).

Ethnicity may also have an effect that is independent of the effect of body composition (Albu et al., 1997; Hayter and Henry, 1994; Liu et al., 1994; Wong et al., 1996). In addition, the climate to which an individual is acclimated may affect BMR. Some recent work (Henry and Rees, 1991; Piers and Shetty, 1993) has indicated that equations developed from a predominantly European population can substantially overestimate the BMR of "tropical peoples." Other research fails to confirm this finding in Indians living in Bangalore, India (Ferro et al., 1997; Soares et al., 1993) and in recent migrants from tropical environments to the United Kingdom (Hayter and Henry, 1993).

Malnourishment may also affect BMR, although exactly what mechanism is involved is still unknown. Some studies have observed that malnourished individuals have decreased RMR (Shetty, 1984; Velthuis te Wierik et al., 1995), while others have indicated that malnourishment does not effect BMR or Em (Ferro et al., 1997; Spurr and Reina, 1986). Also, previously obese individuals who lost weight through nutritional energy restriction have decreased RMR even after their nutritional intake is no longer restricted (Buscemi et al., 1996). The amount of body mass that an individual has lost as a consequence of restricted energy intake seems to also have a role in how severe the decrease in RMR is (Heshka et al., 1990).

In addition to those factors affecting BMR, other factors may affect Em. Uneven terrain probably increases Em, as do inclines and steep declines (Pandolf et al., 1977). Older people use more energy in walking than younger adults do (Voorips et al., 1993). Loads carried by an individual increase the energy that they use in locomotion and the location of the load on the body has a large effect on the amount of the increase in Em (Datta et al., 1973; Keren et al., 1981; Myles and Saunders, 1979; Pandolf et al., 1977; Yu and Lu, 1990). Loads which are carried near the body center of gravity increase Em less than loads which are carried on the extremities (Legg and Mahanty, 1985; Myers and Steudel, 1985). Habituation to load carriage may decrease Em (Maloiy et al., 1986). Jones et al. (1994) found that African pygmies were apparently able to carry heavier loads than Europeans without increasing their Em. It is unclear whether this effect is due to intrinsic characteristics of the Africans, habituation to load carrying, or vari-

ability in body composition. Body proportions (for instance, relative height or leg length to body mass) may also affect Em, though this effect has been difficult to establish (Cavanagh and Kram, 1989; Cavanagh and Williams, 1982; FAO/WHO/UNU, 1985; Ferretti et al., 1991; Owen et al., 1990; Steudel, 1994).

METHODS

Calculation of Em

Adult Em was determined in this research by using the equation developed by Pandolf et al. (1977). The Pandolf equation is superior for this research to similar equations developed by other researchers for several reasons. First, the Pandolf equation provides a method for calculating the energy used when walking while carrying a load; the other curves do not. Since the crux of this research is the comparison between a mother carrying her child (a load) and the mother and child walking independently, using the Pandolf curve allows for consistency. This consistency helps eliminate any spurious differences caused solely by using different ways of calculating LEE. Another reason for using the Pandolf curve is that in the Pandolf equation energy is related to velocity by a squared term. Other researchers use linear regression to express the relationship between energy and velocity. Because one component of energy usage is the movement of the limbs (W_{int}), energy and velocity should be nonlinearly related. When walking, the limbs of a human move similar to pendula and the energy required to move a pendulum is proportional to the velocity squared (Meriam, 1978). In addition, the Pandolf equation is sufficiently general to represent any human mother rather than a particular mother who is a member of a distinctive ethnic group.

The calculation of children's Em is more complex than that of adults because no empirical equation exists for very young children. To overcome this problem, I used the ratio developed by Cavagna et al. (1983) of W_{ext} of adults and children to develop an Em curve for children by using the ratio as a correction factor to the Pandolf et al. (1977) adult curve. In other words, I factored the adult value of Em by the ratio of the W_{ext} of children to the W_{ext} of adults to determine the children's Em.

$$Em_{children} = Em_{adult} * \frac{Wext_{children}}{Wext_{adult}}. \qquad (2)$$

Inherent in this approach is the assumption that the ratio of the W_{ext} of children to W_{ext} of adults is the same as the ratio of Em of children to Em of adults for each age group. Since W_{ext} is only one component of the energy used, this assumption might be fallacious; however, the vertical movement of the body center of gravity is a significant portion of the total energy used in walking. This correction factor approach is necessary because no empirical data are available on Em of young children. When such data exist, this research may need to be modified.

Selection of descriptors of the mother and child

Body masses of the mother and child were selected to represent "normal" variations. Three values of mothers' mass were used to represent small (45 kg), medium (60 kg), and large (75 kg) women. In order to avoid the potentially confounding effects of malnourishment or obesity, these three idealizations must vary in height in order to maintain normal body mass indices (BMI). To determine the BMR of the 45 kg mother, I assumed a stature of 1.5 m (BMI = 20 kg/m^2), while for the 60 kg mother I used 1.65 m (BMI = 22 kg/m^2), and for the 75 kg mother I used 1.8 m (BMI = 23 kg/m^2). In each case, the individual is within her desirable weight for height range (FAO/WHO/UNU, 1985). In addition, I assumed that the standard equations presented in FAO/WHO/UNU (1985) needed no correction for ethnicity or climate. I also assumed that the mother was between 18 and 30 years of age. Child mass was calculated as the average of the median weights for boys and girls ages 1–6 years (FAO/WHO/UNU, 1985).

Locomotor energy expenditure

Locomotor energy expenditure (LEE) is a measure of how much metabolic energy a person uses while moving. It is different from Em because the effect of BMR and the energy required to stand (Es) has been

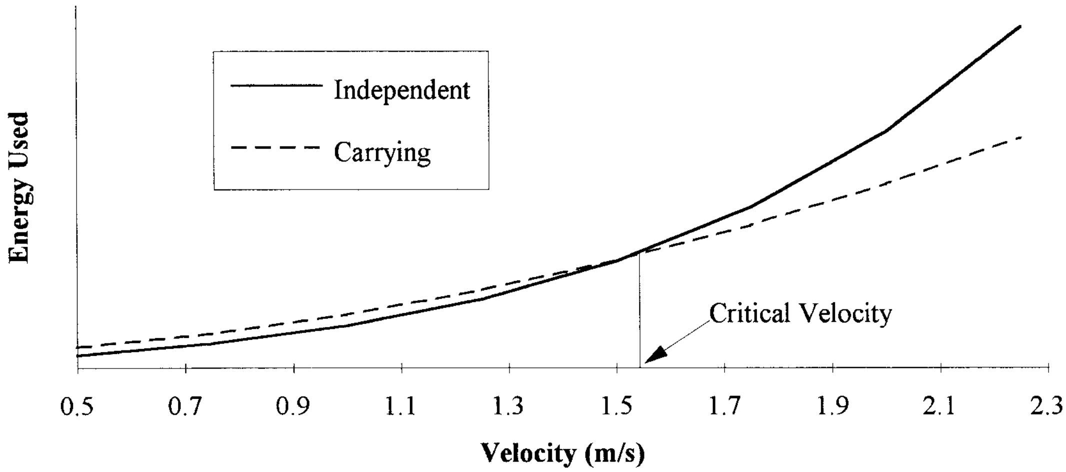

Fig. 4. Critical velocity.

removed. This is an important distinction because BMR can potentially vary independently from LEE. An expanded form of the Pandolf et al. (1977) curve is used to calculate the total energy expenditure. BMR and Es for the mother and her child are obtained from the standard equations presented in FAO/WHO/UNU (1985: Annex 1, Table A; Section 6, Table 5; and Annex 5). Equations 5b and 5c are the average of the equations for male and female children in the appropriate age group. The equations for energy and metabolic rate are given in units of mlO_2/s. For reference,

$$\text{LEE} = \text{Pandolf} - (\text{BMR} + \text{Es}) \tag{3}$$

$$\text{Pandolf} = 0.075\text{BW} + 0.10(\text{BW} + \text{L})\left(\frac{\text{L}}{\text{BW}}\right)^2 + 0.075(\text{BW} + \text{L})(\text{V}^2) \tag{4}$$

$$(\text{BMR} + \text{Es})_{\text{mother}} = (0.032\text{BW} + 0.8047\text{H} + 0.0841) * 1.5 \tag{5a}$$

$$(\text{BMR} + \text{Es})_{\text{child (1–3 years)}} = (0.146\text{BW} - 0.126) * 1.5 \tag{5b}$$

$$(\text{BMR} + \text{Es})_{\text{child (4–6 years)}} = (0.054\text{BW} - 1.20) * 1.5 \tag{5c}$$

where: BW = Body mass in kg; L = Load carried in kg; V = Velocity in m/s; H = Height in m.

When a mother and child each locomote independently, the total LEE is the sum of the LEE of the mother and the LEE of the child.

$$\begin{aligned}\text{Total LEE (independent)} &= (\text{Pandolf (L} = 0) - (\text{BMR} + \text{Es}))_{\text{mother}} \\ &\quad + (\text{correction factor} * \text{Pandolf (L} = 0) - \text{RMR})_{\text{child}}.\end{aligned} \tag{6}$$

When the child is carried, total LEE is the LEE of the mother carrying a load equal to the child's mass.

$$\text{Total LEE (carrying)} = (\text{Pandolf (L} = \text{child's mass}) - (\text{BMR} + \text{Es}))_{\text{mother}}. \tag{7}$$

Calculation of the critical velocity

The critical velocity is that speed at which the LEE of the mother and child walking independently exactly equals the LEE of the mother carrying the child. Above this velocity the dyad expends less energy if the child is carried, while below the critical velocity less energy is expended by the pair if each locomote independently. Figure 4 illustrates this relationship. Critical velocity can be best calculated by iteration.

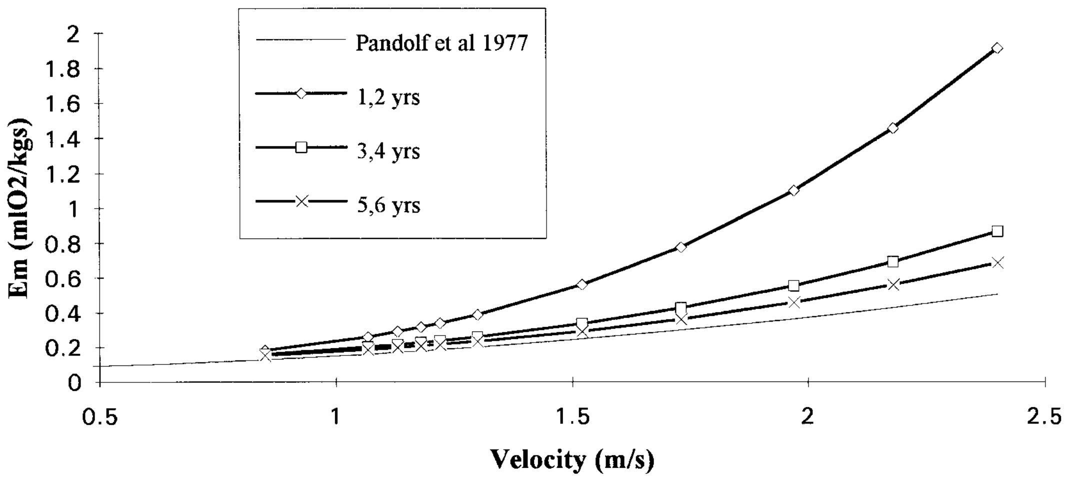

Fig. 5. Young children's energy to walk versus velocity using correction factor.

Other variations

The effect of the mother carrying burdens in addition to the child can be simulated by setting L = the mass of the burden in Equation 6 and by adding the mass of the additional burden to the child's mass in Equation 7. The effect of the child receiving external nutritional support—whether from its father, grandparents, other relatives, governmental agencies, or other sources—can be simulated by discounting the child's contribution in Equation 6, giving Equation 8. Equation 7 remains unchanged because the discounting factor only affects the energy that the child spends, and in the carrying situation that Equation 7 represents, the child is not expending any locomotor energy.

$$\begin{aligned}\text{Total LEE (independent)}\\ &= (\text{Pandolf}\ (L = 0)\\ &\quad - (\text{BMR} + \text{Es}))_{\text{mother}}\\ &\quad + \text{discount} * (\text{correction factor}\\ &\quad * \text{Pandolf}\ (L = 0)\\ &\quad - (\text{BMR} + \text{Es}))_{\text{child}}.\end{aligned} \tag{8}$$

RESULTS

Correction factor

The results of applying the correction factor to the Pandolf curve are shown in Figure 5 for children ages 1–6 years. As can be readily seen, children just beginning to walk are very inefficient when compared to adults, while older children are intermediate between adults and toddlers. For all children, the difference between adult and child becomes more pronounced as velocity increases. It should be pointed out that the curves shown in Figure 5 are based on idealizations of what would happen if a young child did walk at a particular velocity and are not meant to imply that a young child could walk at that speed.

Using my correction factor approach, the 7–8-year-olds in Figure 6 are only slightly less efficient than adults and the children attain essentially adult efficiencies by 9–10 years old. The curve from Waters et al. (1988) for children 6–11 years old, however, suggests that the children should be more inefficient than my correction factor approach predicts. If this same trend is present in younger children, then the energy predictions made in the following sections would underestimate the energy expended by young children to locomote. This would tend to decrease the critical velocity at which the mother should switch from carrying to forcing her child to walk.

General hypotheses

From evaluation of Equations 6 and 7, several general hypotheses can be generated.

1. Younger children should be carried at lower velocities than older children. This

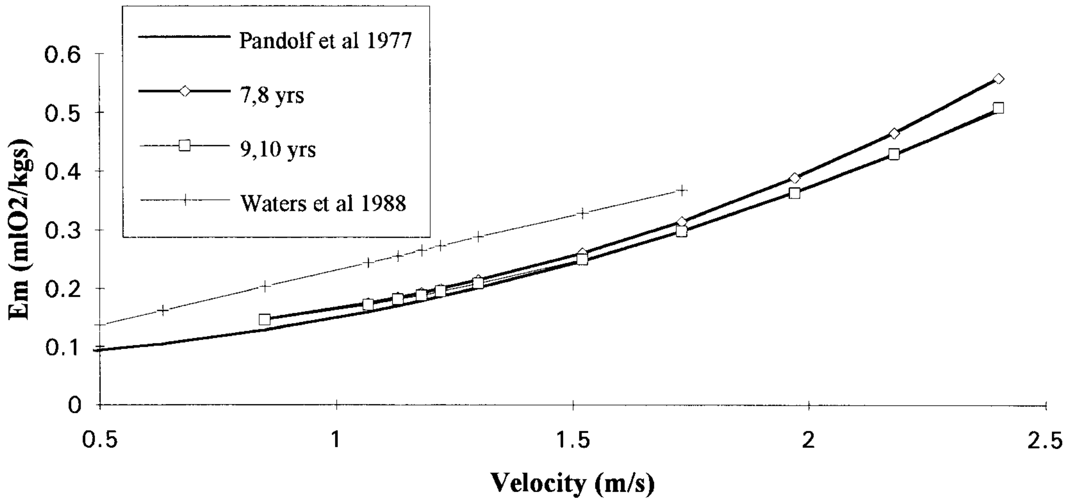

Fig. 6. Children's energy to walk versus velocity using correction factor.

TABLE 1. Critical velocity

Critical velocity (m/sec)		Child					
		1–2-Year-olds		3–4-Year-olds		5–6-Year-olds	
	Weight	9.85 kg	12.3 kg	14.35 kg	16.35 kg	18.20 kg	20.10 kg
Mother	45 kg	1.2	1.3	1.8	1.9	2.1	2.3
	60 kg	1.0	1.1	1.4	1.5	1.7	1.8
	75 kg	0.8	0.8	1.1	1.2	1.3	1.4

relationship should hold even if the younger child weighs the same as the older child. This effect is caused by the greater immaturity of the gait of the younger child and the consequently greater energy they spend to locomote.

2. Lighter mothers should force their children to walk at higher velocities than heavier mothers. This holds for all ages and masses of children.
3. Heavier children should be forced to walk at higher velocities than lighter children of the same age. The second and third hypotheses occur because the energy consumed by carrying is proportional to the mass of the load divided by the mass of the person carrying the load (Equation 4). Decreasing the mother's mass or increasing the child's mass functions to increase the energy spent in carrying.

In addition to these general hypotheses, specific predictions can be made for particular situations. Knowing the age of the child and the masses of mother and child, the critical velocity can be determined and walking–carrying patterns can be estimated.

Critical velocity

Table 1 gives the critical velocities for several mother–child combinations. Interestingly, the simulations would indicate that mothers should begin to force their children to walk an appreciable amount of time around 3 years old, because normal adult walking velocity is 1.36 m/s (Waters et al., 1988). Before age 2, no mother–child dyad would benefit from the child walking independently at the normal adult walking velocity. At age 3, only the heaviest mother would still benefit from carrying her child at the normal adult velocity.

Effect of added load

Table 2 is similar to Table 1 but it gives the critical velocities for various values of added load (in addition to the child). The

TABLE 2. Critical velocity with extra load

Critical velocity (m/sec)		Child's age and weight					
		1–2-Year-olds		3–4-Year-olds		5–6-Year-olds	
Mother's weight (kg)	Load (kg)	9.85 kg	12.3 kg	14.35 kg	16.35 kg	18.20 kg	20.10 kg
45	0.0	1.2	1.3	1.8	1.9	2.1	2.3
	5.0	1.2	1.3	1.7	1.8	2.1	2.1
	10.0	1.2	1.3	1.7	1.8	2.0	2.1
	15.0	1.2	1.3	1.6	1.7	1.9	2.0
	20.0	1.2	1.3	1.6	1.7	1.9	2.0
60	0.0	0.9	1.0	1.4	1.5	1.7	1.8
	5.0	1.0	1.0	1.4	1.4	1.6	1.7
	10.0	1.0	1.0	1.3	1.4	1.6	1.7
	15.0	1.0	1.0	1.3	1.4	1.6	1.6
	20.0	1.0	1.0	1.3	1.4	1.6	1.6
75	0.0	0.8	0.8	1.1	1.2	1.3	1.4
	5.0	0.8	0.9	1.1	1.2	1.3	1.4
	10.0	0.8	0.9	1.1	1.2	1.3	1.4
	15.0	0.8	0.9	1.1	1.2	1.3	1.4
	20.0	0.8	0.9	1.1	1.2	1.3	1.4

TABLE 3. Critical velocity for various levels of maternal support

Critical velocity (m/sec)		Child's age and weight					
		1–2-Year-olds		3–4-Year-olds		5–6-Year-olds	
Mother's weight (kg)	Maternal support (%)	9.85 kg	12.3 kg	14.35 kg	16.35 kg	18.20 kg	20.10 kg
45	100	1.2	1.3	1.8	1.9	2.1	2.3
	75	1.3	1.4	2.0	2.0	—	—
	50	1.5	1.6	—	—	—	—
	25	1.8	2.0	—	—	—	—
60	100	0.9	1.0	1.4	1.5	1.7	1.8
	75	1.0	1.1	1.5	1.6	1.9	2.0
	50	1.2	1.3	1.8	1.9	2.2	—
	25	1.5	1.6	—	—	—	—
75	100	0.8	0.8	1.1	1.2	1.3	1.4
	75	0.8	0.9	1.3	1.3	1.5	1.6
	50	1.0	1.1	1.5	1.5	1.8	1.9
	25	1.3	1.3	1.9	—	—	—

most readily apparent aspect of Table 2 is that loads in addition to the child's weight do not significantly change the critical velocity. For both the 45 kg and 60 kg mothers with a 1- or 2-year-old child, critical velocity is unchanged by the addition of burdens, while with older children the critical velocity decreases with increasing load. For a 75 kg mother, the critical velocities do not change with increasing load. In all cases, the changes in critical velocity with increasing additional burden are small.

Effect of child supported by other agencies

To show the effect of external support, I have calculated critical velocity for each mother–child combination for 100, 75, 50, and 25% maternal contribution to the child's nutritional intake. These simulations are shown in Table 3. When the child has an external source of nutritional support, the critical velocity is increased for all combinations of mother and child masses. In general, the mother will force her supported child to walk independently at higher velocities than she would an unsupported child. Another way of looking at this is that the age of the child decreases for a given critical velocity. A 60 kg mother might carry her unsupported 3-year-old child at the average adult walking velocity of 1.36 m/s, but should force that child to walk independently if it receives external support. The effect of support is most pronounced for the lightest (45 kg) mother and least for the heaviest (75 kg) mother, as shown in Table 3. For the lightest (45 kg) mother, it quickly becomes in her

best interest to not carry her child. If her child receives 50% of its support from another source, the 45 kg mother should not carry her toddler when she locomotes at average adult walking velocity. In the case of the 60 kg mother, if she provides 100% support, she should begin to force her child to walk around 3 years old, while if she provides that same child with only 25% of its support, she should never carry it. The heaviest (75 kg) mother will always carry her 1–2 year old at normal adult walking velocity, but at low levels of support she should force children older than 3 years to walk. Figure 7 graphically demonstrates these trends. In general, when the child is supported by an outside agency, the mother requires him/her to spend a larger portion of her/his own energy in transportation. When the mother provides no nutritional intake to her child, it is never in her best energetic interest to carry the child.

DISCUSSION

Nutritional intake ultimately provides the energy that the body uses to maintain itself and to perform all the necessary metabolic and behavioral tasks that are required to survive and reproduce. Despite this fact, it is important to note that nutritional intake and energy are not synonymous. Instead, they are only secondarily related to each other. While inadequate nutrition may limit the energy available to an individual, ad libitum nutritional intake does not necessarily lead to infinite energy reserves that are available for fueling locomotor tasks (Saris, 1995). Nutritional intake may be influenced by nutrient needs and not solely by the need to maximize energy acquisition (Kaplan and Hill, 1992). In addition, as long as there are opportunity costs associated with the procurement or storage of energy or energy is a limiting factor on fertility or mortality, then optimal use of energy will be favored even when food is not scarce (Kaplan and Hill, 1992; Smith, 1983). This research is, therefore, applicable to mothers in almost all ecological environments because energy is a costly, limiting, and finite resource even when nutritional intake is optimal (Smith, 1983). Malnourishment may make the choices more difficult because the energy budget of the mother is smaller; however, the decision rules that govern the allocation process are appropriate in most ecological circumstances. Prolonged malnourishment does have one obvious effect on this research in that it decreases maternal and offspring body mass.

The mother and child are engaged in a complex evolutionary relationship and a distinct conflict of interest occurs in many aspects of their interactions (Trivers, 1974). On the one hand, this research was completed from the perspective of the mother; in some scenarios it is to her advantage to carry her child, while in other situations it is energetically less expensive for her to force the child to walk independently. On the other hand, it is always in the child's energetic best interest to be carried because the child's energy reserves are finite and the energy that he/she expends in walking independently cannot be used for other metabolic and behaviorally important tasks like growing. From this theoretical conflict, a physical conflict may stem and mothers may have to force their children to walk. This sets up yet another potential conflict: the velocity with which the mother walks most efficiently may not coincide with the most efficient speed for the child. Therefore, to the three hypotheses regarding critical velocities I would add two additional ones:

4. Mothers will have to force their children to walk independently and the children may resist their mother's attempts to force them.
5. Mothers and their children may not agree on a velocity for walking.

I want to reiterate that all five hypotheses and all of this discussion are predicated on the assumption that energetic considerations are paramount. Obviously, a child who never walks has created an untenable behavioral handicap for himself that is unlikely to be favored from either a proximate or ultimate perspective.

As Altmann and Samuels (1992) observed in their study of feral baboons, mothers will carry their offspring at higher velocities and will force their offspring to walk independently at lower velocities. This "decision" is made based on energetics and the critical

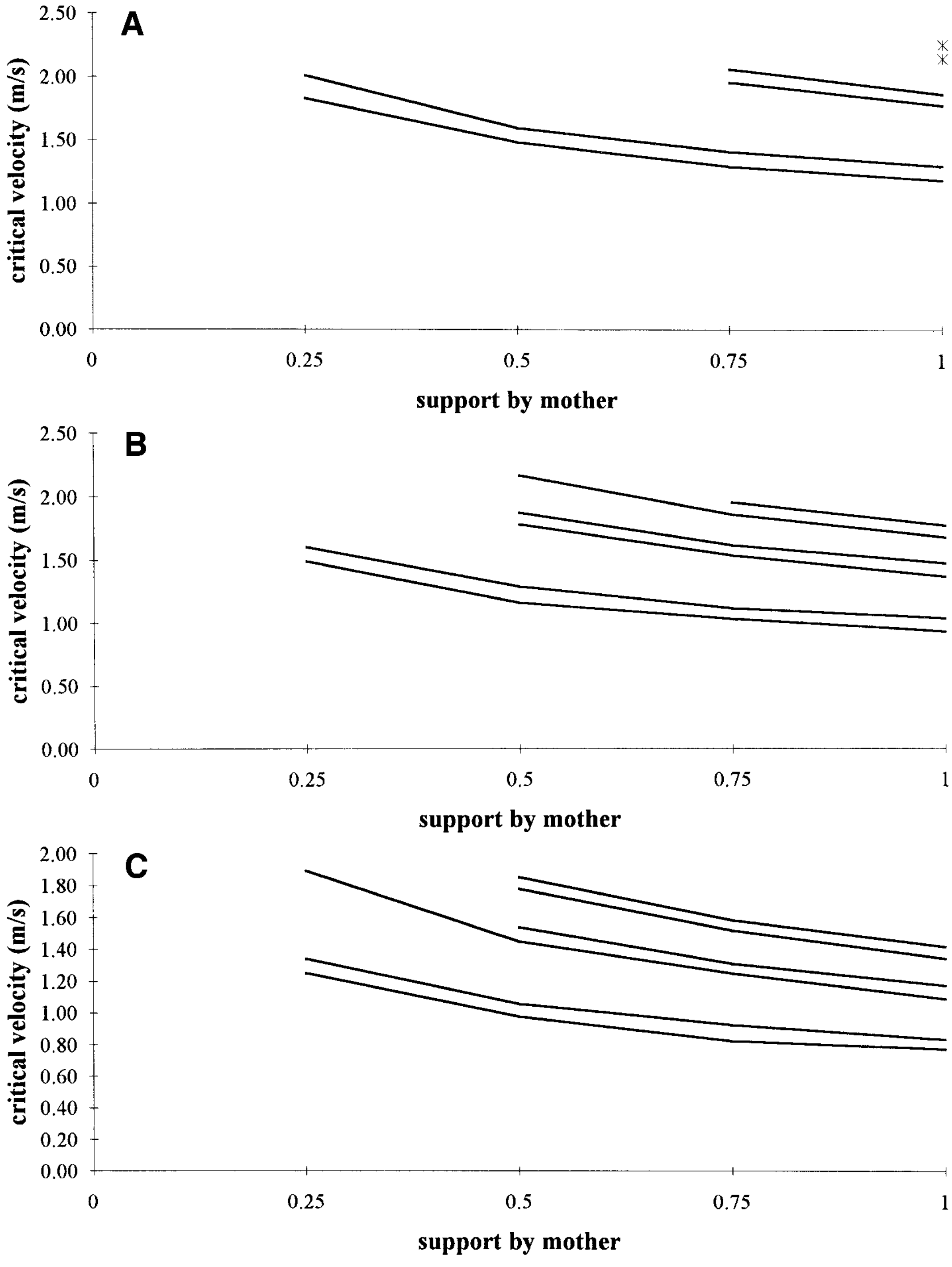

Fig. 7. Critical velocity with varying levels of child support. Top line represents 6-year-old child while bottom line represents 1-year-old child. Child's age decreases 1 year for each line. **(A)** 45 kg mother; **(B)** 60 kg mother; **(C)** 75 kg mother.

velocity depends on the masses of the mother and the child and the child's age. It should be noted that while the critical velocity is a single point, mothers and their children will walk in a range of velocities, depending on the particular circumstances in which they find themselves. On any given day, a mother should carry her child when she walks above the critical velocity and force the child to walk when they are traveling at speeds below the critical velocity. If the average adult walking velocity is taken as a simplified indicator of the amount of time that a mother spends carrying her child, then Table 1 indicates that the 45 kg mother will begin to force her child to walk an appreciable amount of the time around age 2 years. The 60 kg mother delays this decision until the child is 3 years old, while the 75 kg mother waits until the child is 5 to 6 years old before she forces her to walk independently most of the time. The addition of burdens in excess of the weight of the child does not change this picture appreciably, as Table 2 shows. The addition of nutritional support to the child does, however, radically modify the ages when the mother would force her child to walk independently, as Table 3 indicates. In all cases, as the contribution of the mother to the child's nutritional support, and hence energetic budget, decreases, the critical velocity increases and the age at which she would force her child to walk independently decreases. In other words, increased nutritional support of offspring by external agencies reduces the mother's need to carry her child. As mentioned previously, if the mother provides no support, then it is never in her energetic best interest to carry her child.

These findings may have significant consequences for interbirth intervals (IBI) and corresponds quite well with a 4-year IBI. Once the present child is capable of independent locomotion at normal adult walking velocities without undue energetic expenditure, the mother can concentrate her energy on another child. In the classic Trivers (1974) scenario, parental investment in the current offspring comes at a cost to future offspring. Energy expenditure to carry a child may limit the mother's available energy to invest in another offspring. Only after the present child is able to locomote reasonably efficiently can the mother afford to invest in another youngster. Even with children as old as 5–6 years, some mothers with unsupported children might benefit from carrying them at fast walking speeds ($>$1.7 m/s). As indicated earlier, children do not approach adult efficiencies until they reach at least 7–8 years old, but even though their gaits are not completely mature, children of this age would seldom be carried. It is important to note that while nutritional support from agencies other than the mother decreases the age at which the mother will force her child to walk independently, support does not necessarily decrease the absolute amount of energy that the mother contributes to the child. At the critical velocity, the mother is still contributing the same amount of energy in either the carrying or independent walking scenarios. It is only the velocity and, consequently, the age of the child for a particular velocity of interest that changes. What support does accomplish, however, is the freeing of the mother from the act of carrying her toddler, perhaps allowing her to carry a younger child.

The logical extension of this theoretical research would be to test the five hypotheses presented herein by evaluating child transport decisions of women and their offspring. This test would be best accomplished in a nonWestern environment without the complications of automobiles, baby strollers, and other transport mechanisms. If this theoretical approach is tested in a real situation, energetic equations appropriate to the population and individual under investigation must be utilized. At a minimum, age, sex, weight, height, nutritional status, location, and ethnicity should be accounted for when BMR is determined. Empirical determination of both BMR and Em may be warranted if the population of interest differs substantially from the reference populations.

The energy used by mothers to transport their dependent young can be a significant maternal investment and may seriously affect the ability of the mother to invest in other offspring. As such, an understanding of this energy usage is vital to our understanding of maternal investment as well as to the evolution of our unique locomotor form.

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